FOREST GROWING PATTERNS AND MATHEMATICAL MODELS (Theory of Biomathematics and Its Applications XII : Mathematical and experimental approach to clarify patterns in a transition process)

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1. Introduction

Recent empirical researches are going to notify in the forest dynamics that not only intra-species competition among trees but also inter-species competition between trees and grass plays an important role. The latter competition together with the former might provide the natures of forest dynamics like discontinuous moving front edges of trees, meta stability of forest ecosystem and so on, see [1, 5, 7, 8, 9, 10]. This Note is then devoted to introducing a continuous model describing the tree-grass competition ecosystem as a reaction-diffusion system. We also show that the existing model presented in [6] by Kuznetsov et al. can be derived from the new one by some reasonable modifications.

2. Tree-Grass competition model

We consider a tree-grass ecosystem in a fixed domain $\Omega \subset \mathbb{R}^2$. For the trees, we assume a life cycle of seeds, seedlings, young age trees and old age trees. These densities at position $x \in \Omega$ and time $t \in [0, \infty)$ are denoted by $w(x,t)$, $s(x,t)$, $u(x,t)$ and $v(x,t)$, respectively. In the meantime, as the life cycle of grass is extremely short with respect to trees, we will ignore it and denote simply by $g(x,t)$ its biomass at position $x \in \Omega$ and time $t \in [0, \infty)$.

Our modeling assumptions are the followings.

(1) The interception rate of radiation by the canopy of old age trees over the young trees is given by $[1 - e^{-k_v v}]$ with some exponent $k_v > 0$. Such a formula is called Beer's law.
(2) The interception rate of radiation by the canopy of old age trees and that of young age trees over the layer of grass is given by $[1 - e^{-k_u u} e^{-k_v v}]$ with some exponent $k_u > 0$.
(3) Similarly, the interception rate of radiation by old age trees, young age trees and grass over seedlings is given by $[1 - e^{-k_g g} e^{-k_u u} e^{-k_v v}]$ with some exponent $k_g > 0$.
(4) It is known that trees that cannot grow die at a high rate. So, the death rate of young age trees is assumed to be proportional to $[1 - e^{-k_v v}]$.
(5) The death rate of grass is assumed to be proportional to $[1 - e^{-k_u u} e^{-k_v v}]$.
(6) The death rate of seedlings is assumed to be proportional to $[1 - e^{-k_g g} e^{-k_u u} e^{-k_v v}]$.
(7) The growth of grass obeys a logistic-diffusion equation.

Under these assumptions, we present the following initial-boundary value problem for a reaction-diffusion system:

$$
(2.1)\qquad \begin{cases}
\dfrac{\partial s}{\partial t} = \beta\delta w - f_s s - \gamma_s \left[1 - e^{-k_g g} e^{-k_u u} e^{-k_v v}\right] s & \text{in } \Omega \times (0,\infty),\\
\dfrac{\partial u}{\partial t} = f_s s - f_u u - \gamma_u \left[1 - e^{-k_v v}\right] u & \text{in } \Omega \times (0,\infty),\\
\dfrac{\partial v}{\partial t} = f_u u - h v & \text{in } \Omega \times (0,\infty),\\
\dfrac{\partial w}{\partial t} = d_w \Delta w - \beta w + \alpha v & \text{in } \Omega \times (0,\infty),\\
\dfrac{\partial g}{\partial t} = d_g \Delta g + \tau \left(1 - \dfrac{g}{K}\right) g - \gamma_g \left[1 - e^{-k_u u} e^{-k_v v}\right] g & \text{in } \Omega \times (0,\infty),\\
\dfrac{\partial w}{\partial n} = \dfrac{\partial g}{\partial n} = 0 & \text{on } \partial\Omega \times (0,\infty),\\
s(x,0) = s_0(x),\ u(x,0) = u_0(x),\ v(x,0) = v_0(x),\\
\qquad\qquad w(x,0) = w_0(x),\ g(x,0) = g_0(x) & \text{in } \Omega.
\end{cases}
$$

Here, f_s and f_u are aging rates of seedlings and young age trees, respectively. γ_s, γ_u and γ_g are coefficients of death rate of seedlings, young age trees and grass, respectively; and h is a death rate of old age trees. α is a production rate of seeds; β is a deposition rate of seeds; and δ is an establishment rate of seeds. K is a capacity of Ω for the grass which is a constant and τ is a growth rate of grass. d_w and d_g are diffusion coefficients of seeds and grass, respectively. Seed density and grass biomass are assumed to satisfy the homogeneous Neumann boundary conditions on the boundary $\partial\Omega$ of Ω.

3. Simplification of (2.1)

Let us simplify the model by two steps.

First, we unify the young and old ages of trees into a single age. Thereby these trees inherit the properties of young and old age trees. The seedlings grow into trees, the canopy of trees intercept radiation over the layer of grass and they produce seeds.

We then obtain the following reaction-diffusion system:

$$
(3.1)\qquad \begin{cases}
\dfrac{\partial s}{\partial t} = \beta\delta w - f_s s - \gamma_s \left[1 - e^{-k_g g} e^{-k_v v}\right] s & \text{in } \Omega \times (0,\infty),\\
\dfrac{\partial v}{\partial t} = f_s s - h v & \text{in } \Omega \times (0,\infty),\\
\dfrac{\partial w}{\partial t} = d_w \Delta w - \beta w + \alpha v & \text{in } \Omega \times (0,\infty),\\
\dfrac{\partial g}{\partial t} = d_g \Delta g + \tau \left(1 - \dfrac{g}{K}\right) g - \gamma_g \left[1 - e^{-k_v v}\right] g & \text{in } \Omega \times (0,\infty),\\
\dfrac{\partial w}{\partial n} = \dfrac{\partial g}{\partial n} = 0 & \text{on } \partial\Omega \times (0,\infty),\\
s(x,0) = s_0(x),\ v(x,0) = v_0(x),\ w(x,0) = w_0(x),\\
\qquad\qquad g(x,0) = g_0(x) & \text{in } \Omega.
\end{cases}
$$

In addition to this unification, we further assume that the reaction coefficients τ and γ_g in the growth equation for g are sufficiently large. Then, the equation for g may be reduced to a transcendental equation

$$\tau\left(1-\frac{g}{K}\right)g-\gamma_g\left[1-e^{-k_v v}\right]g=0 \qquad \text{in} \quad \Omega\times(0,\infty).$$

Consequently, g is represented by v with the function

$$\begin{aligned} g &= \varphi(v) \\ &\equiv K\left\{1-\gamma\left[1-e^{-k_v v}\right]\right\}, \qquad 0\le v<\infty, \end{aligned}$$

where we put $\gamma=\frac{\gamma_g}{\tau}$. Since $\varphi(v)$ is monotonously decreasing and since $\varphi(+\infty)=K(1-\gamma)$, we must assume that

$$\gamma<1, \text{ i.e., } \gamma_g<\tau. \tag{3.2}$$

Under (3.2), the equation for grass is now eliminated and (3.1) reads as

$$\begin{cases} \dfrac{\partial s}{\partial t}=\beta\delta w-f_s s-\gamma_s\left[1-e^{-k_g\varphi(v)}e^{-k_v v}\right]s & \text{in} \quad \Omega\times(0,\infty), \\ \dfrac{\partial v}{\partial t}=f_s s-hv & \text{in} \quad \Omega\times(0,\infty), \\ \dfrac{\partial w}{\partial t}=d_w\Delta w-\beta w+\alpha v & \text{in} \quad \Omega\times(0,\infty), \\ \dfrac{\partial w}{\partial n}=0 & \text{on} \quad \partial\Omega\times(0,\infty), \\ s(x,0)=s_0(x),\ v(x,0)=v_0(x),\ w(x,0)=w_0(x) & \text{in} \quad \Omega. \end{cases} \tag{3.3}$$

4. Comparison of (3.3) with classical model

Let us recall the classical forest kinematic model that has been presented by Kuznetsov, Antonovsky, Biktashev and Aponina in 1994. According to [6] their model is given by

$$\begin{cases} \dfrac{\partial u}{\partial t}=\beta\delta w-fu-\gamma(v)u & \text{in} \quad \Omega\times(0,\infty), \\ \dfrac{\partial v}{\partial t}=fu-hv & \text{in} \quad \Omega\times(0,\infty), \\ \dfrac{\partial w}{\partial t}=d\Delta w-\beta w+\alpha v & \text{in} \quad \Omega\times(0,\infty), \\ \dfrac{\partial w}{\partial n}=0 & \text{on} \quad \partial\Omega\times(0,\infty), \\ u(x,0)=u_0(x),\ v(x,0)=v_0(x),\ w(x,0)=w_0(x) & \text{in} \quad \Omega. \end{cases} \tag{4.1}$$

Here, u denotes density of young age trees and v that of old age trees in Ω. $\gamma(v)$ denotes a death rate of young age trees which depends on the density of old age trees v. The authors assumed that $\gamma(v)$ is possibly given as a quadratic function

$$\gamma(v)=a(v-b)^2+c, \qquad 0\le v<\infty, \tag{4.2}$$

with positive constants a, b and c. That is, $\gamma(v)$ hits its minimum at a certain density of v. They say that this assumption has been derived from some experimental results. But it still seems that we have to discuss more on the death function $\gamma(v)$, because $\gamma(v)u$ is the only nonlinear term in (4.1).

In (3.3) we rewrite the state variable s into u. Then, the mortality of seedlings is given by $-\Phi(v)u$, here

$$\Phi(v) = \gamma_s \left[1 - e^{-k_g\varphi(v)}e^{-k_v v}\right], \qquad 0 \le v < \infty. \tag{4.3}$$

The derivative of $\Phi(v)$ is written by

$$\Phi'(v) = \gamma_s k_v e^{-k_g\varphi(v)}e^{-k_v v}\left[1 - K\gamma k_g e^{-k_v v}\right].$$

Therefore, if we assume, in addition to (3.2), the relation

$$K\gamma k_g > 1, \text{ i.e., } K\gamma_g k_k > \tau, \tag{4.4}$$

then $\Phi(v)$ hits its minimum at a single point $\overline{v}$ which is given by

$$\overline{v} = \frac{\log(K\gamma k_g)}{k_v}.$$

After some computations, we verify that

$$\Phi(\overline{v}) = \gamma_s \left\{1 - \frac{e^{-[Kk_g(1-\gamma)+1]}}{K\gamma k_g}\right\}$$

(note (3.2)). Furthermore, we compute the second derivative of $\Phi(v)$ at $v = \overline{v}$. Indeed, it is given by

$$\Phi''(\overline{v}) = \frac{\gamma_s k_v^2 e^{-[Kk_g(1-\gamma)+1]}}{K\gamma k_g}.$$

Thus we have observed that, under (3.2) and (4.4), the death function $\Phi(v)$ in (4.3) can be approximated by a square function of the form (4.2) with

$$a = \tfrac{1}{2}\Phi''(\overline{v}), \quad b = \overline{v}, \quad c = \Phi(\overline{v})$$

in a neighborhood of $\overline{v}$.

The classical model (4.1) have already been studied extensively by [2, 3, 4], see also [11, Chapter 11]. It is in fact known that the asymptotic behavior of solutions changes drastically depending on the parameters in the equations, especially on a, b and c. The results obtained here then provide some suggestions how these important parameters are determined from other measurable ecological parameters.

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